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Utilisation of the Commonwealth Potato Collection in potato breeding

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Summary

The use of the Commonwealth Potato Collection in potato breeding is set in the context of the evolution of the crop and the need to widen its genetic base by introgression and base broadening. The introduction of the potato to Europe and its subsequent worldwide spread is described. An introduction is given to the world's major potato genebanks, and the current status of the Commonwealth Potato Collection is presented. Material from this genebank has been extensively used to improve the potato. Work on wild species as sources of resistance to late blight started before the genebank was initiated, and since then CPC accessions have provided major R-genes and durable resistance to breeders, greatly benefiting growers and consumers of the potato. Progress identifying and exploiting resistance to viruses and potato cyst nematodes is described. New sources of further pest and disease resistance genes are present in the germplasm in the collection, offering the potential to overcome current and future pests and diseases. Use of the cultivated species in the collection for base broadening is described and discussed. The collection also harbours a wide range of quality traits of use to breeders, including variation for cooking and crisping, anthocyanins, carotenoids, ascorbate metabolism and others. As breeding and genetics become more precise, and as both the knowledge of biochemical pathways and means of analysing chemical composition advance, new ways of accessing this variation become possible. Possible strategies to achieve these goals are discussed.

Introduction

Potato domestication, evolution and breeding from a narrow genetic base

One or a few closely related and inter-fertile tuber-bearing *Solanum* species were domesticated in the Andes of southern Peru and northern Bolivia over 7000 years ago (Hawkes, 1990). The result was diploid *S. stenotomum*, also referred to as a form of *S. tuberosum* (Group Stenotomum), from which other cultivated species were derived, including diploid *S. phureja* (or Group Phureja), tetraploid *S. tuberosum* subsp. *andigena* (or Group Andigena) and tetraploid *S. tuberosum* subsp. *tuberosum* (or Group Tuberosum). Andigena potatoes became the most widely grown form in South America. Tuberosum potatoes were selected from Andigena types for tuber production in long days in Chile and are referred to as Chilean Tuberosum. Phureja potatoes were selected from Stenotomum for lack of tuber dormancy and faster tuber development so that up to three crops per year could be grown in the lower, warmer, eastern valleys of the Andes. Tetraploid by diploid crosses can give tetraploid offspring as a result of a 'triploid block' and the diploid producing *2n* unreduced gametes. Hence Andigena, Tuberosum, Stenotomum and Phureja can be regarded as an inter-fertile cultivated gene pool.

Andigena potatoes were introduced into the Canary Isles around 1562 and from there to mainland Europe in the 1570s (Hawkes & Francisco-Ortega, 1993). As the growing of potatoes spread north eastwards across Europe, the potato became adapted to the long summer days of northern Europe and evolved sufficiently

to be classified as subspecies *tuberosum*, albeit with Andigena cytoplasm. Starting in the 17th century, potatoes were taken from Europe and cultivated in many other parts of the world (Pandey & Kaushik, 2003). Today, potatoes are grown in 149 countries from latitudes 65°N to 50°S and at altitudes from sea level to 4000 m (Hijmans, 2001), and the potato is the fourth most important food crop after wheat, maize and rice (Lang, 2001).

Potato breeding in the modern sense began in 1807 in England when Knight made deliberate hybridizations between varieties by artificial pollination (Knight, 1807). It flourished in Britain and elsewhere during the second half of the 19th century when many new cultivars were selected and propagated by farmers and hobby breeders. A single Chilean Tuberosum cultivar, Rough Purple Chili, was introduced into the USA in 1851 (Goodrich, 1863), and its descendents were widely employed as female parents in crosses with European Tuberosum at the end of the 19th century, following losses from the late blight epidemics in Europe and North America during the 1840s (Hawkes, 1990). Hence Chilean Tuberosum cytoplasm predominates in modern cultivars. The Tuberosum form of cultivated potato was thus founded on a narrow genetic base compared with that available in its centre of origin and in wild species. As a consequence, it lacked genes for adequate levels of resistance to a number of pests and pathogens which became problems once it had assumed its role of a staple food. Furthermore, by the beginning of the 20th century, the narrow genetic base was starting to impede more general progress in potato breeding.

This paper reviews the establishment and utilisation of the Commonwealth Potato Collection in broadening the genetic base of potato breeding. While references are made to other collections and research, no attempt has been made to do a comprehensive review of these topics.

Germplasm collections including the Commonwealth Potato Collection

Recognition of Central and South America as the centres of origin and diversity of the tuber-bearing members of the genus *Solanum* resulted in numerous collecting expeditions, from those pioneered by the Russians in the 1920s (Hawkes, 1990) to the more recent ones of the 1990s (Spooner & Hijmans, 2001). These, in turn, led to the establishment of a number of potato germplasm collections worldwide (Bradshaw, 2000), including the world collection at the International Potato Centre (CIP, Lima, Peru), the Dutch-German Potato Collection (CGN, Wageningen, The Netherlands), the Groß Lüsewitz Potato Collection (GLKS, IPK, Groß Lüsewitz, Germany), the Potato Collection of the Vavilov Institute (VIR, St Petersburg, Russia), the US Potato Genebank (NRSP-6, Sturgeon Bay, USA), Potato Collections in Argentina, Bolivia and Peru and the Commonwealth Potato Collection (CPC) which is now held at SCRI, Dundee, Scotland (Hawkes, 1990).

The CPC dates back to an expedition to Mexico by plant collector E.K. Balls in 1938 and to another more extensive one to South America in 1939 which was commissioned by the Imperial Agricultural Bureaux of the United Kingdom government. The 1939 expedition was led by E.K. Balls who was accompanied by potato specialist J.G. Hawkes (Hawkes, 1951). During the years 1941–1948 the collection was assessed at the Potato Virus Research Station in Cambridge and the wild species shown to have useful resistances to late blight, viruses, cyst nematodes and frost. During the period 1948–1951 Hawkes collected in Mexico and sent material back to the CPC (Hawkes, 1990). Extra collections of cultivated diploids were added in the 1960s by Dodds, Simmonds and Paxman. Since the mid-1960s the entire collection has been maintained and stored in botanical seed form. During the 1990s it was expanded by the incorporation of the personal collection of wild and cultivated potatoes amassed by Professor Hawkes and held at Birmingham University. This collection was started with an expedition to the USA, Mexico and Central America in 1958 and followed up with ones to South America over the period to 1981 (Hawkes, 1990).

Today the CPC comprises about 1300 accessions of which two-thirds are wild and one-third are cultivated species. The collection includes 77 of the 228 wild tuber-bearing *Solanum* species recognised by Hawkes (1990). It has been comprehensively screened for the absence of true seed borne diseases and a substantial part of the collection meets the most stringent of European quarantine standards for plant health. Plant material, normally in the form of true seed, is available to researchers and breeders under agreements consistent with the provisions of the Convention on Biodiversity and the International Undertaking on Plant Genetic Resources for Food and Agriculture. Details of the holdings can be seen at the CPC website (http://www.scri.sari.ac.uk/cpc/) and a database of all European collections is available

here: http://www.cgn.wageningen-ur.nl/pgr/research/eupotato/.

Introgression of desirable genes from the CPC

Late blight

Late blight (*Phytophthora infestans* (Mont.) de Bary) first made its impact outside of Mexico in the mid-1840s when severe epidemics swept through North America and Europe and resulted in the Irish potato famine (Large, 1940).

The use of *S. demissum* as a source of resistance to late blight predates the CPC. For example, at the Scottish Plant Breeding Station (SPBS), in 1932 Dr Black crossed *S. demissum* (6x) as female parent with the first cultivar from SPBS, The Alness (4x), and secured a pentaploid (5x) clone from which he was able to introgress major dominant R-genes for blight resistance. Later, in 1937, he secured a few artifical tetraploid seedlings by hybridising *S. phureja* (2x) with *S. demissum* (6x) and used them in genetical studies and his breeding programme (Black, 1970). Pentland Ace (*R3*) came from the cross made in 1937 and was released in 1951 after just three backcrosses to Tuberosum. However, the commercially more successful Pentland Dell (*R1, R2, R3*) took five generations and was released in 1960 (Bradshaw, 2000). The *S. demissum* used by Black was added to the CPC as accession CPC 2127. Whilst the major R-genes from *S. demissum* failed to provide durable resistance, further selection for quantitative field resistance resulted in the release of cultivar Torridon in 1987 and Stirling in 1991 (Bradshaw et al., 1995).

Viruses

Degeneration in potato crops over successive vegetative generations was recognised by Salaman (1921) to be the result of virus infection and led to targeted breeding for resistance from the 1930s onwards (Solomon-Blackburn & Barker, 2001). This involved the screening of germplasm collections including the CPC for sources of resistance. Genes conferring resistance in a non-specific manner were preferred and the following proved particularly useful: *Rx* genes for extreme resistance to PVX from Andigena (CPC 1673) and from *S. acaule* (CPC 379); *Ny* genes for hypersensitive resistance to PVY from *S. demissum* (CPC 4) and *S. microdontum* (CPC 51a), both in a background of field resistance from *S. phureja* (CPC 979), and from *S. chacoense* (CPC 51b, same gene as in 51a but in different background); and *Ry* gene for extreme resistance to PVY from *S. stoloniferum* (CPC 9 and 28.4, but hybrid MPI 61.303/34 from Cologne, Germany was a more commonly used source). The genes have provided durable resistance.

Potato cyst nematodes

Breeding for resistance to the golden (*Globodera rostochiensis*) and white (*G. pallida*) potato cyst nematodes provides a good set of examples of the timescale involved in the utilisation of the CPC (Bradshaw et al., 2004a). The two species of nematode originate from the Andean regions of South America with *G. pallida* commoner north of Lake Titicaca and *G. rostochiensis* south of this lake (Evans et al., 1975). They were first found in Europe about 120 years ago and started to become a serious problem in the UK in the early 1950s (Bradshaw et al., 2004a).

The first source of resistance to be used successfully came from a CPC accession (CPC 1673) of Andigena potatoes. It proved to be a simply inherited dominant major gene which was named *H1*, from the old name for the nematode *Heterodera*, and which was effective against what are now known as pathotypes Ro1 and Ro4 of *G. rostochiensis.* Following a cross between CPC 1673 and cultivar Kerr's Pink in 1952, it took three backcrosses to the European cultivated potato, with selection for commercially desirable traits as well as for PCN resistance in nematode-infested soil, before Pentland Javelin was released from SPBS in 1967. The Plant Breeding Institute (PBI), Cambridge, had achieved the same feat a year earlier with Maris Piper. Having incorporated the *H1* gene into a number of cultivars and breeding lines, these can be intercrossed in a breeding programme and offspring sought with two copies of the gene, through test crosses to a susceptible line. These duplex lines can, in turn, be intercrossed and offspring sought with three or four copies of the *H1* gene. Whilst only one copy is required for resistance, such clones are extremely useful as parents in a breeding programme because all, or nearly all, of their progeny are resistant even when the other parent is susceptible, thus avoiding the need to screen the progeny for resistance or waste resources on raising susceptible seedlings. Thus Pentland Javelin was crossed with Maris Piper and clone 10341ab18 selected as having two copies of *H1*, then 10341ab18 was crossed with Cara (which has one copy of *H1*) and 15205ab6

selected as having three copies of *H1*. Finally 15205ab6 was crossed with Picasso (two copies of *H1*) and clone 92PD39a5 selected and National Listed in 2004 as a new early maincrop cultivar Vales Sovereign. The resistance has proved durable in the UK where Ro1 appears to be the only pathotype, but pathotypes such as Ro3, which can overcome *H1*, have been found on the European mainland.

PCN populations which could overcome the *H1* gene were soon found, and proved to be what is now known as pathotype Pa2/3 of *G. pallida.* Quantitative resistance to both *G. pallida* and *G. rostochiensis* was found in a diploid wild species from South America, *S. vernei* (CPC 2487 and CPC 2488). Colchicine treatment of these and another *S. vernei* produced tetraploid plants of *S. vernei* which were crossed with Tuberosum potatoes in 1957 and 1958. The resulting hybrids were intercrossed and also outcrossed to other cultivars and clones for four generations with selection for PCN resistance and other desirable traits, before cultivars Morag and Glenna were released in 1985 and 1987, respectively. Whilst these were commercially acceptable cultivars, it took longer to produce a cultivar with the potential to be commercially successful. Clone 10300(13), a parent of Glenna, was crossed with Cara to produce clone 15119ac5. Then clone 8204a4, with *S. demissum* derived field resistance to late blight, was crossed with 15119ac5 to produce clone 88P43(5) which was National Listed as cultivar Lady Balfour in 2001. It is an organic maincrop variety with blight and PCN resistance. Santé from the Netherlands and Nadine from Caithness Breeders are other examples of cultivars with PCN resistance from *S. vernei.*

The third main source of resistance to be successfully incorporated into the European potato was quantitative resistance to *G. pallida*, but not to *G. rostochiensis*, from Andigena (CPC 2802), and is known as *H3*. Starting in 1969, a self from CPC 2802 was crossed with Maris Piper, followed by three backcrosses to Tuberosum to give clones 12601ab1, 12674ab1 and 14069a4, the last of which was National Listed as cultivar Eden in 1991. However, again a further generation was required to produce a cultivar with the potential to be commercially successful. Cara was crossed with 12674ab1 in 1988 to produce clone 88P24d51 which was in its second year of National List trials in 2004 as cultivar Vales Everest. It is a maincrop potato which is suitable for processing. Fortuitously, clones 12601ab1, 12674ab1 and 14069a4 will also produce light coloured fry products after storage at 4 °C, an important processing trait.

The CPC, therefore, is typical of potato germplasm collections in that disease and pest resistance have been introgressed from wild and cultivated species, but relatively few species have been used to any extent in the breeding of successful modern cultivars (Ross, 1986), and there have been mixed fortunes with the durability of resistance.

Genetics of resistance

During the period 1990–2001, 19 single dominant genes (R genes) and a number of Quantitative Trait Loci (QTL) for resistance to fungi, viruses and nematodes were positioned on the molecular map of potato using DNA markers (Gebhardt & Valkonen, 2001). These included some of the genes mentioned in the previous section: *R1* (on chromosome 5), *R2* (on chromosome 4) and *R3, R6*, and *R7* (on chromosome 11) for resistance to late blight; *Rx1* (from Andigena, on chromosome 12) and *Rx2* (from *S. acaule*, on chromosome 5) for resistance to virus PVX; *Ry* (from *S. stoloniferum*, on chromosome 11) for resistance to virus PVY and *H1* (on chromosome 5) for resistance to *G. rostochiensis* pathotypes Ro1 and Ro4. More recently, Bradshaw et al. (2004b) have analysed the blight resistance of cultivar Stirling and found a QTL on chromosome 4 which explained 37% of the variation in foliage blight scores in a cross with susceptible clone 12601ab1. Likewise, Bryan et al. (2002, 2004) found QTLs for resistance to *G. pallida* on chromosomes 5 and 9 in germplasm derived from *S. vernei* (CPC 2487 and 2488) and on chromosomes 4 and 11 in clone 12601ab1 which was derived from Andigena (CPC 2802).

Increased knowledge about the inheritance of resistance genes and QTLs should allow more effective use of them in breeding programmes including molecular marker-assisted selection. Kasai et al. (2000) have developed SCAR markers to the PVY resistance gene *Ry* (from Andigena, on chromosome 11). They should be powerful tools in marker-assisted selection as they showed high accuracy for detection of the *Ry* gene and one marker RYSC3 was generated only in genotypes carrying *Ry*, namely 14 out of 103 breeding lines and cultivars with diverse genetic backgrounds. Bakker et al. (2004) have identified an AFLP marker (EM1) which co-segregates with the *H1* gene for resistance to *G. rostochiensis* pathotype Ro1. EM1 and *H1* were present in 19 resistant cultivars and absent from 26 susceptible ones. However, Bakker et al. (2004) recommended conversion to a CAPS marker

for use in marker-assisted selection as such markers are cheaper and easier to handle. A marker linked to the QTL for *G. pallida* resistance on chromosome 5 was converted to a single-locus PCR-based marker and shown to detect the presence of the QTL in diploid and tetraploid potato germplasm (Bryan et al., 2002). As there was good evidence that it was specific to an introgressed segment of DNA from *S. vernei*, it should prove useful in marker-assisted selection for the QTL.

New sources of resistance

Late blight

Since 1984, new populations of *P. infestans* have been spreading from Mexico to the rest of the world (Goodwin & Drenth, 1997) and are seen as a new threat to food security, because they comprise both mating types, more aggressive strains and resistance to the widely used fungicide metalaxyl. The presence of both mating types means that there is the possibility of sexual reproduction resulting in oospores which can overwinter in soil and start epidemics earlier each season, as well as faster evolution of strains capable of overcoming cultivar resistance. These increasing threats prompted further surveys of the CPC for new sources of resistance.

Limited screenings from 1986 to 1995 identified high levels of foliage resistance in seven Mexican (*S. pinnatisectum* CPC 3559, *S. polyadenium* CPC 3501, *S. verrucosum* CPC 54, *S. papita* CPC 2639, 2640, 3214, and 3997, *S. polytrichon* CPC 3987 and 7072, *S. stoloniferum* CPC 9 and 28, and *S. brachycarpum* CPC 7027 and 7032) and one Bolivian (*S. circaeifolium* CPC 7089) species (Bradshaw et al., 1995).

More extensive screenings of 301 accessions with complex race 1,2,3,4,6,7 of *P. infestans* were subsequently performed by Ramsay et al. (1999) who found 36 to be very resistant (Table 1). They came from 15 of the 58 species tested and were in six taxonomic series with 30 accessions from Mexico and six from Bolivia and Argentina. Interestingly, when Van Soest et al. (1984) screened the German-Netherlands Potato Collection they found species with high levels of resistance concentrated in the Mexican and Bolivian-Argentinian parts of the centres of diversity of the potato. They identified 24 accessions with very high levels of resistance in eight taxonomic series: Bulbocastana, Pinnatisecta, Commersonii, Circaeifolia, Demissa, Longipedicellata, Polyadenia and Tuberosa.

Potato cyst nematodes

Although the *H1* gene for resistance to *G. rostochiensis* and the quantitative resistances to *G. pallida* should

Table 1. Accessions from the CPC very resistant to blight (Arg = Argentina, Bol = Bolivia, Bra = Brazil, Chi = Chile, Mex = Mexico, Par = Paraquay, Uru = Uruguay, USA; data from Ramsay et al. (1999))

Species	Country	Series	Accession
S. alandiae	Arg/Bol/Chi	Tuberosa	7324
S. berthaultii	Bol	Tuberosa	3607, 4036
S. cardiophyllum	Mex	Pinnatisecta	7510
S. chacoense	Arg/Bol/Par/Uru	Yungasensia	7211
S. commersonii	Arg/Bra/Uru	Commersoniana	5858
S. demissum	Mex	Demissa	2102, 2103
S. fendleri	Mex/USA	Longipedicellata	4020
S. hougasii	Mex	Demissa	7049, 7050
S. iopetalum	Mex	Demissa	7055
S. microdontum	Arg	Tuberosa	4048
S. polytrichon	Mex	Longipedicellata	7087
S. papita	Mex	Longipedicellata	7076, 7077, 7078, 7079, 7080, 7083, 7084, 7085
S. semidemissum	Mex	Demissa	7103
S. stoloniferum	Mex	Longipedicellata	9, 1332, 2093, 2243, 2619, 2713, 2714, 4013, 4018, 7082, 7113, 7197
S. verrucosum	Mex	Tuberosa	7213

remain useful in the UK for the immediate future, in the longer term new sources of more durable resistance are almost certainly going to be required. Turner (1989) screened 35 species in the CPC for new sources of resistance to *G. rostochiensis* and *G. pallida* and found resistance to Ro1-5 and Pa1-3 in *S. kurtzianum* (CPC 3783), *S. sparsipilum* (CPC 3488, 3562 and 3563), *S. stenotomum* (CPC 2688) and *S. stenotomum* × *S. spegazzinii* (CPC 4711). More recently Castelli et al. (2003) screened 198 accessions from 63 species in the previously untested germplasm in the CPC which came from Hawkes' personal collection. With *G. pallida* (Pa2/3) roughly equal distributions of resistant and susceptible accessions were found throughout South America and Mexico, whereas with *G. rostochiensis* (Ro1) the majority of resistant accessions originated from the southern part of South America, mainly Argentina (the origin of *G. rostochiensis*). A high proportion (37%) of accessions were resistant to both species of nematode including ones from five *Solanum* species in which resistance had not previously been reported: *S. brevidens*, now known as *S. palustre*, (CPC 7135), *S. mochiquense* (CPC 7062), *S. neocardenasii* (CPC 7208), *S. okadae* (CPC 7129) and *S. semidemissum* (CPC 7112). The accessions with resistance to a number of populations of both nematode species, and hence the most promising for use in breeding programmes, were *S. canasense* (CPC 7142), *S. gourlayi* (CPC 7161), *S. okadae* (CPC 7327), *S. spegazzinii* (CPC 7195) and *S. verrucosum* (CPC 7130) (Castelli, 2003). When Van Soest et al. (1983) screened the German-Netherlands Potato Collection, they found resistance to several pathotypes of cyst nematodes in *S. gourlayi* (Ro5, Pa1-3), *S. multidissectum* (Ro1-3,5, Pa2,3), *S. oplocense* (Pa2/3), *S. spegazzinii* (Ro1,3,5, Pa2,3), *S. sucrense* (Ro1,2,5, Pa1-3) and *S. vernei* (Ro1-3,5, Pa1-5). They also found that at altitudes between 2500 and 4250 m, the Altiplano and Cordillera oriental of Peru, Bolivia and Argentina were rich sources of species with resistance to *G. pallida.*

Other traits

Small-scale and mostly unpublished studies indicate that there are sources of resistance to other pests and diseases in the CPC as well as to frost. For example, resistance to wart (*Synchytrichium endobioticum* (Schilb.) Perc.) is found in *S. stoloniferum* CPC 1331 and 10 accesssions of Group Andigena. Examples of resistance to aphids, blackleg and *Fusarium* species causing dry rot (Wastie & Bradshaw, 1995) are also recorded.

Sexual and somatic hybridization of *S. tuberosum* with wild species

Prospects are good for the rapid introgression into Tuberosum of these new sources of disease and pest resistance and desirable alleles for other traits. Today, by manipulating ploidy and with due regard to the endosperm balance number (EBN), virtually any potato species can be utilized in such introgression (Ortiz, 1998, 2001). The schemes used for ploidy level manipulations exploit the facts that unreduced 2*n* gametes are common in *Solanum* species and maternal haploids (dihaploids) of tetraploid *S. tuberosum* can be extracted following crosses with pollinator clones of *S. phureja*, thus allowing breeding at the diploid level before returning to the tetraploid level for cultivar production (Carputo & Barone, 2005; Jansky et al., 1990). Furthermore, Wenzel et al. (1979) proposed the combination of haploidy, somatic (protoplast) fusion and classical breeding steps for combining several traits of potato in an analytical synthetic manner. Somatic fusion has also allowed the production of hybrids between diploid EBN1 species and tetraploid EBN4 Tuberosum, for example, the non-tuber bearing species *S. brevidens* which has tuber soft rot and early blight resistances (Tek et al., 2004) and *S. bulbocastanum* which has a major gene for broad spectrum resistance to late blight (Naess et al., 2000).

Molecular marker-assisted introgression

The genetical analysis of new sources of economically important traits will allow the location of underlying major genes and QTLs on the molecular map of potatoes and breeding strategies to be designed for the fast and efficient transfer of desirable alleles to Tuberosum using molecular marker-assisted selection. For example, if one was starting the introgression of PCN resistance from *S. vernei* today, it would be known that there are two QTLs, one on chromosome 5 and the other on chromosome 9, and that *S. vernei* will cross with dihaploids of Tuberosum because both are diploids with an EBN of two. It would be preferable to do the introgression at the diploid rather than the tetraploid level because the complete elimination of unwanted alleles and whole chromosomes from the wild species is faster at

Table 2. Increase in the frequency of recurrent parent allele (a), homozygosity (aa in diploid 2x and aaaa in tetraploid 4x assuming chromosomal inheritance), and whole chromosomes (two from recurrent parent in diploid and four in tetraploid) when one or two crossovers per bivalent in backcrosses to aa and aaaa starting with Aa and AAaa (the exact frequency allows for recombination producing whole chromosome of recurrent parent)

Backcross generation	Frequency of allele		Frequency of homozygote		Minimum frequency of whole chromosome one crossover		Exact frequency of whole chromosome one crossover	Minimum frequency of whole chromosome two crossovers
	4x	2x	4x	2x	4x	2x	2x	2x
1	75.0	75.0	16.7	50.0	4.2	25.0	25.0	12.5
2	87.5	87.5	52.8	75.0	20.3	43.8	50.0	23.4
3	93.8	93.8	75.5	87.5	37.3	57.8	68.8	33.0
4	96.9	96.9	87.6	93.8	51.9	68.4	81.3	41.4
5	98.4	98.4	93.8	96.9	63.5	76.3	87.5	48.7
6	99.2	99.2	96.9	98.4	72.5	82.2	90.6	55.1

the diploid level, unlike the change in allele frequency which is the same (Table 2). While phenotypic selection could be practised for PCN resistance and against unwanted wild species traits, one would have the additional options of selecting phenotypically or genotypically for PCN resistance and genotypically against the wild species genome (e.g. against offspring with the most *S. vernei*-specific AFLPs) as suggested by Ramsay et al. (1999) and Iovene et al. (2004). Furthermore, with adequate molecular coverage of all 12 chromosomes, it is possible to select in a very precise way for the desirable products of meiosis in each backcross generation. Whichever method was chosen, genetical knowledge coupled with that of chiasmata frequency and distribution and the properties of the binomial distribution, would allow the estimation of the optimal combination of population sizes and number of backcross generations (Hospital, 2003). For *S. vernei* PCN resistance, three backcrosses with population sizes in the hundreds is realistic and could be achieved with adequate PCN screening in 6 years, which is much less than actually occurred without the use of molecular markers.

Where introgression is performed at the tetraploid level, the result may not be a genotype with 48 Tuberosum chromosomes including one or more with the introgressed gene(s). The SCRI blight-resistant cultivar Torridon, mentioned earlier, was found to have 50 chromosomes (Wilkinson, 1992). The result of the introgression from *S. brevidens* referred to above was a high yielding clone, C75-5+297, with resistances to both tuber soft rot and early blight. Using both molecular and cytogenetic approaches, Tek et al. (2004) showed that C75-5+297 had 47 chromosomes, including four copies of chromosome 8, three from potato and one from *S. brevidens* which was the only part of the wild species genome present. In contrast, Barone et al. (2001) did obtain 48 chromosomes and evidence of recombination between *S. commersonii* (an EBN1 diploid) and *S. tuberosum* chromosomes in their molecular marker-assisted introgression of tuber soft rot resistance.

Gene cloning

As potatoes are heterozygous outbreeders, use of the same recurrent parent during introgression would result in a self of the recurrent parent and hence inbreeding depression. This can be avoided by using different Tuberosum parents for each backcross but would result in an entirely new cultivar, which may or may not be the desired outcome. The only way to introduce a gene into a known cultivar is by the transgenic route. Hence the molecular cloning of natural resistance genes and their transfer into well-adapted but susceptible cultivars is being pursued in a number of laboratories worldwide. The *Rx* (Andigena) gene in cultivar Cara has been genetically delimited within a bacterial artificial chromosome (BAC) clone and stably introduced into the susceptible cultivar Maris Bard by *Agrobacterium*-mediated transformation (Bendahmane et al., 1999). The transgenic *Rx*-mediated resistance was indistinguishable from the *Rx*-mediated phenotype in cultivar Cara. The *R1* gene for resistance to late blight has been cloned and introduced into the susceptible cultivar

Desiree and shown to give a typical hypersensitive response (HR), similar to the resistant line hosting *R1* (Ballvora et al., 2002). Likewise, the *RB* and *Rpi-blb1* genes (which are allelic) from *S. bulbocastanum* have been cloned and introduced into the susceptible cultivars Katahdin and Impala, respectively, and shown to confer broad spectrum resistance to late blight (Song et al., 2003; van der Vossen et al., 2003). Most recently, Paal et al. (2004) have cloned the *Gro1* gene for resistance to *G. rostochiensis* from *S. spegazzinii* and introduced it into the susceptible cultivar Desiree and shown that it confers resistance to pathotype Ro1.

Base broadening

As mentioned earlier, the Tuberosum form of cultivated potato was founded on a narrow genetic base compared with that available in Latin America where the International Potato Center (CIP) has been able to assemble a collection of 3527 unique native cultivars (Huaman et al., 1997). Hence in 1959, a long-term selection experiment was started in the UK by Simmonds (1969) with one objective of producing Andigena parents suitable for incorporation into potato breeding programmes. A gene pool of Andigena potatoes with origins approximately 45% Bolivian, 35% south Peruvian, 10% north Peruvian and 10% Colombian accessions from the CPC was subjected to recurrent mass selection in outdoor plots. Within four generations, Simmonds (1969) reported good progress, with the better Andigena clones comparable in yield and maturity to Tuberosum cultivars and better on average in terms of late blight resistance. These clones were more variable in tuber shape than modern cultivars and inferior in regularity of tuber shape, but of similar cooking quality. As a consequence of their rather "rough" appearance, it subsequently proved rather more difficult to breed successful cultivars from crosses of this Neo-Tuberosum material with intensively selected Tuberosum clones. A number of other programmes worldwide have also demonstrated that through simple mass selection under northern-latitude, long-day summer conditions, Andigena will adapt and produce parents suitable for direct incorporation into modern potato breeding programmes (Bradshaw & Mackay, 1994).

The original mass-selected Neo-Tuberosum population was retained and a bulk seed harvest taken for long-term storage. This biodiverse population has now been recovered, tested for current quarantine diseases, and is entering research programmes at SCRI using the latest molecular approaches. An important question that now arises is whether it should be selected for further improvement, particularly in tuber shape and appearance, or maintained without conscious selection as a biodiverse but day neutral (for tubering) population. In the genomics age, a biodiverse population that could be used as a source of desirable alleles for marker-assisted breeding is an attractive proposition.

During the period 1962–1979, Carroll (1982) also employed a mass selection method to produce a long-day adapted population of Group Phureja (with a small contribution from other diploid cultivated material) from CPC accessions. The population rapidly adapted to long-day conditions and yield improved over several generations, mainly as a result of increase in tuber size without a reduction in tuber numbers. It was also possible to demonstrate variation for late blight resistance and to select for this in the field. The proportion of oval/long oval, regular-shaped tubers increased, but further selection is required for improved dormancy if the material is to provide a broad-based population for direct use in breeding finished cultivars. Nevertheless, hybridisation of members of this improved diploid population with tetraploid Tuberosum cultivars via unreduced pollen grains did produce tetraploid hybrids which were superior to standard tetraploid cultivars in both total and marketable yield, generally producing more tubers per plant with slightly lower mean tuber weights (Carroll & De Maine, 1989). Furthermore, since 2001, three diploid Phureja clones have been added to the UK National List as cultivars Mayan Gold, Inca Sun and Inca Dawn. Their yields are lower than tetraploid Tuberosum cultivars, so they are being targeted at niche markets for their flavour attributes. The SCRI collection of long-day Phureja clones is proving extremely useful for genetical research as it contains a range of useful traits including high levels of tuber carotenoids, improved flavour, reduced cooking times and resistance to *Erwinia* (De Maine et al., 2000). Haynes and Christ (1999) have reported similar progress and interest in a long-day-adapted population of *S. phureja* and *S. stenotomum* which was developed in the USA.

Future use of the CPC in the genomics age

In all crops, the development of molecular tools and the deeper understanding emerging of gene structure and function has driven the reawakening of an interest

in exploiting germplasm collections. Potatoes are in a particularly advantageous position to benefit from these advances, as there is a particularly wide range of diversity in both cultivated and cross-compatible wild relatives. Therefore, at SCRI, a comprehensive molecular genetic analysis of the CPC is being performed to determine overall genetic structure, a better understanding of the genome origins of the allopolyploid species and a better appreciation of between and within accession diversity. The AFLP analyses have been completed and organelle-derived marker analyses and gene sequence analyses are now underway. It has already been possible to show that not all of the groupings of species as described by traditional taxonomy are valid. For example, the species in series Megistacroloba fall into three groups interlaced between other diploid species. Furthermore, determination of the origin of the different genomes within allopolyploid groups is now possible using precise methods such as the sequencing of single genes in allopolyploids and possible diploid progenitors, opening the prospect of more refined searches for novelty among the available germplasm. As molecular methods become more efficient, and working on large scales more practical, new ways of exploring and exploiting germplasm become possible. Given that small blocks of linked DNA sequence are likely to persist through the mixing and recombination which has taken place since domestication, it may become feasible to explore the variation in germplasm collections such as the CPC by whole-genome scans using densely saturating markers. As the persistence of the linkage disequilibrium which permits such an approach depends on the structure of the population analysed, it is possible that not only the collection itself but also the populations derived from it can be explored with such methods in the near future.

Biochemistry and genomics

The last few decades have seen great improvements in our understanding of biochemical pathways in plants and in the accessibility and throughput of biochemical analytical techniques. End-user needs in potato production are influenced increasingly by tuber biochemistry, and new market opportunities exist for potatoes with enhanced nutritional quality. Examples of these biochemical traits include carbohydrate metabolism, affecting cooking and crisping quality, glycoalkaloid levels affecting potential toxicity, and tuber flesh anthocyanin, carotenoid and ascorbate levels and stability affecting nutritional value. Linking together genomics and biochemistry offers great benefits for potato improvement, as reviewed by Dale and Bradshaw (2003) for carbohydrate metabolism and processing traits. Another example is the current research effort at SCRI to identify the genes and alleles responsible for elevated levels of carotenoids. Morris et al. (2004) have already been able to exploit SCRI's long-day-adapted *S. phureja* population to study carotenogenesis during tuber development and storage. They compared the levels of carotenoids in the high carotenoid-accumulating *S. phureja* cultivar Inca Dawn (DB375/1) with two *S. tuberosum* cultivars (Pentland Javelin and Desiree) that accumulate lower levels of tuber carotenoid. We can now seek to exploit natural variants for the trait by looking for an association in sets of germplasm with DNA sequence variants in candidate genes for biosynthesis and turn-over. By this means we can compare alternative candidate positions in pathways and directly determine the gene involved. We expect that this approach will become a useful method for directly determining crucial steps in pathways using existing sets of germplasm and without the need to create traditional segregating populations. The challenge will then be to get desirable alleles into new cultivars and hence farmers' fields as quickly as possible.

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